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Designing freshwater protected areas (FPAs) for indiscriminate fisheries

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ABSTRACT

Freshwater protected areas (FPAs) are increasingly important for biodiversity conservation, given the intensive use of these systems for water, energy and food production. However, the fisheries benefits of FPAs are not well understood, particularly for indiscriminate fisheries typical of tropical systems. Here we report the results of a model that tests the fisheries effects of no-take protected areas in conditions unique to indiscriminate riverine/floodplain systems. The model has a generalized form applicable to a wide range of systems. We report the results of the general model, as well as those from a specialized form parameterized for the Tonle Sap lake, Cambodia. Both the general and Tonle Sap versions of the model show that FPAs can pay important fisheries benefits, especially where it is difficult to control fishing mortality through gear restrictions or other means. The harvest and profit benefit response curves have similar shapes, with additional FPAs paying high dividends at less than approximately 50% FPA coverage, and then truncating and declining thereafter. In the specific setting of the Tonle Sap of Cambodia, FPAs would pay a large increase in harvest because current FPA coverage is low. It may be counterintuitive to community fisheries managers in Cambodia that the best way to increase harvest is to restrict fishing, but at very high levels of fishing effort, reducing effort or area fished will improve both harvest and profit. In Cambodia, it may make sense to maximize harvest rather than profit because fishers living in poverty need to maximize protein offtake, but the benefits of FPAs remain. Similar considerations may apply in many freshwater and indiscriminate fisheries.

1. Introduction

The effects of no-take protected areas on fisheries production and conservation have been studied in marine environments for several decades (Lester et al., 2009; Gaines et al., 2010; Halpern et al., 2009), but with few exceptions, protected areas have largely been ignored in freshwater systems (Hermoso et al., 2016; Saunders et al., 2002; Srinoparatwatana and Hyndes, 2011; Suski and Cooke, 2007). This may be a missed opportunity because many of the conditions that give rise to marine protected area (MPA) success are arguably even more relevant in freshwater systems. In particular, freshwater systems are often marked by high fishing mortality, often combined with indiscriminate fishing (McCann et al., 2015), settings in which freshwater protected areas (FPAs) may offer benefits both to fisheries and to biodiversity conservation (Allan et al., 2005). FPAs are now being tested in a number of freshwater settings (e.g., Srinoparatwatana and Hyndes, 2011) under the premise that they could return fisheries, economic, and ecological benefits. However, their effects on harvest, profits, and conservation are not well understood.

Both theory and empirical studies have shown that when fish stocks are heavily fished, protected areas can act as a substitute for active fishery management in delivering conservation benefits. For example, Hastings and Botsford (2003) showed that MPAs can be as effective as optimized harvest strategies in producing fish yield and fishery-wide conservation, and Lester et al. (2017) showed that MPAs can increase yield and biomass in areas surrounded by open access fishing. These outcomes are a consequence of the buildup of fish biomass inside the protected area, some of which spills out into the adjacent fished area,

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providing a 'fish bank' that delivers dividends over time. Conservation of non-target species often results as well (Lester et al., 2009).

While the conditions under which MPAs deliver positive outcomes in the marine setting are now well-established, almost no research addresses the potential design and fisheries outcomes of protected areas in freshwater settings. Instead, theory and research on FPAs has focused mostly on biodiversity conservation (Suski and Cooke, 2007; Bower et al., 2015). The combined fisheries and biodiversity benefits of FPAs are less often explored. MPA fishery benefits often hinge on the degree to which overfishing is occurring, with more overfished fisheries tending to benefit more from MPAs. The stock recovery and spillover effects noted in some MPAs would be important reasons to consider implementing no-take FPAs, since many freshwater systems are overfished, especially in the tropics. But important differences between freshwater and marine fisheries call into question whether theory and empirical evidence from marine systems can be directly applied to freshwater settings (Bayley, 1995).

Freshwater fisheries are often exploited by small-scale, low-capital fishermen and are protein-maximizing systems, in contrast to many marine fisheries, which are often highly capitalized and may be focused on maximizing profit, rather that subsistence protein (KC et al., 2017). In many freshwater settings in the tropics, profit margins are low and resources for managing the fishery or enforcing gear restrictions or yields are limited (Bayley, 1995). In these settings, fisheries involve many small-scale fishers using equipment of all types and sizes, indiscriminately targeting all available sizes and species of fish (McCann et al., 2015; Allan et al., 2005).

The theory of "indiscriminate fisheries" describes the likely outcomes of offtake in multi-species fisheries (Costello, 2017; McCann et al., 2015). It suggests that indiscriminate fisheries seek to maximize protein production, resulting in systems with higher trophic levels removed, with some systems properties similar to those found in productive monocultures of terrestrial agriculture. These fisheries may be highly sensitive to environmental perturbations, such as climate change, for reasons analogous to those that make crop monocultures vulnerable to drought and disease. These qualities distinguish indiscriminate fisheries from temperate and marine single-species fisheries and call into question whether the theory and practice of MPAs translate directly to these settings.

While freshwater systems cover less than 0.8% of the earth's area (compared to 71% covered by ocean, about 5% of which is covered by MPAs), they provide protein for tens of millions of people worldwide (Abell et al., 2008; Dudgeon et al., 2006; McIntyre et al., 2016). Because these fisheries emphasize volume of offtake over selection of large individuals or specific species, the context for potential protected area benefits to individual fishers is quite different to the environments in which MPAs have been studied. Analyses targeting indiscriminate freshwater fisheries are needed to understand the potential benefits of protected areas in these settings.

We draw our motivation for this analysis from perhaps the prototypical example of an indiscriminate freshwater fishery (McCann et al., 2015): the Tonle Sap in the heart of Cambodia. The Tonle Sap Lake (TSL) is a complex freshwater system that provides protein to over 2 million people (Lim et al., 1999; Lamberts, 2006). It serves as an excellent test case of the fisheries impact of freshwater protected areas, because it closely approximates the conditions described in indiscriminate fisheries theory (McCann et al., 2015). In particular, the fishery emphasizes high harvest volumes (Hall et al., 2006), in a manner analogous to agricultural monocultures, rather than the high-value offtake of select species and sizes which typifies many marine fisheries.

In this paper we make three discrete contributions. First, we examine the theoretical conditions under which an indiscriminate freshwater fishery could benefit from an FPA. Second, we examine a range of potential design features (size, location, number) for a network of FPAs, and show how these designs give rise to different outcomes. Finally, we apply this model to the Tonle Sap to examine whether FPAs are likely to benefit fisheries in one of the world's most prolific freshwater fisheries. For the latter contribution, we find that context matters – the results hinge critically on the degree of cooperation in harvest across different fishing villages situated around the lake. To characterize this, and other key model parameters, we use new survey data and other results from a multi-year multi-disciplinary project on the Tonle Sap ecosystem. We believe that all three contributions are novel, and that these findings will help inform freshwater fisheries management and conservation in a variety of tropical settings.

2. Methods

2.1. Study site description – Tonle Sap Lake (TSL)

The Tonle Sap Lake (TSL) is characterized by high- and low-water seasons. During the high-water season, the floodplain covers a dramatically larger area than in the low-water season. During low-water season, the floodplain size decreases, fish are concentrated in a smaller area, and certain species move into a connected river. TSL currently has a system of community fishing areas (CFis), similar to marine Territorial Use Rights for Fishing (TURFs) (Fig. 1). Over the last two

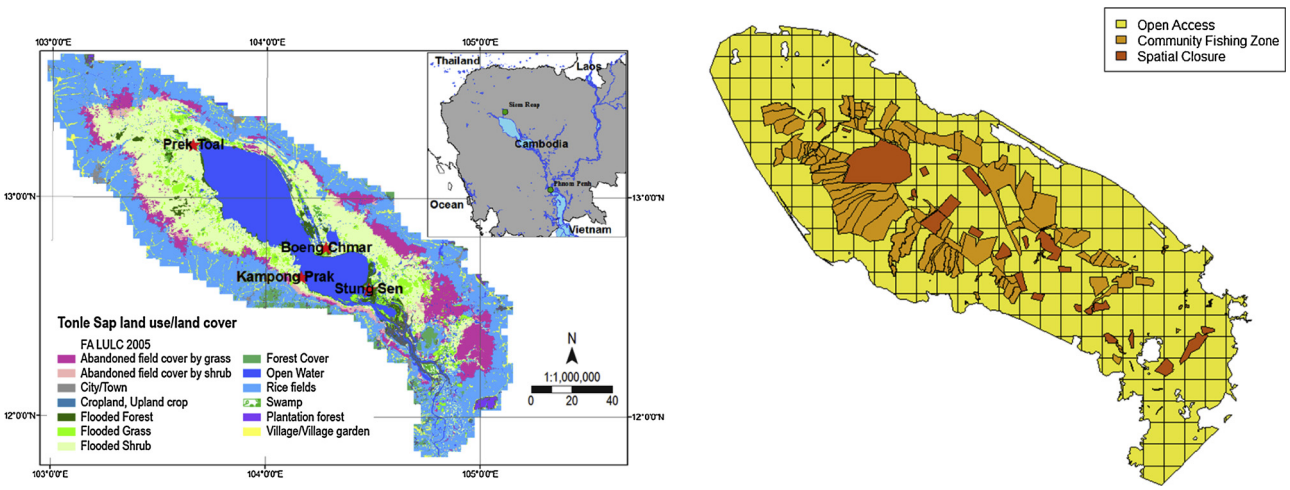

Fig. 1. Habitat map of Tonle Sap and surrounding region (left). Model configuration of current Tonle Sap management (right). Yellow areas are open access, light orange areas are current community fishing zones where fishing mortality is controlled, and dark orange areas are FPAs where fishing is not allowed. All lake cells shown, river cell not shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

decades, a system based on centrally-allocated private-use lease-holds has been replaced by decentralized community-based fisheries management that includes provision for CFis, complemented by conservation zones (CZs) or fish sanctuaries (which we refer to as freshwater protected areas, FPAs) that continue to be centrally managed by the national government.The organization of fishing villages and the implementation of fishery policy affects fishing behavior and they each may act either cooperatively or non-cooperatively in their harvesting strategy. We develop a bioeconomic forecasting model and use it to simulate biomass, harvest, and profit in a forward projection over a 20-year period to explore likely outcomes under current management and under hypothetical scenarios in which management within CFis could be improved, the network of FPAs could be expanded, or both. Management adjustments are currently being considered in the region, and we hope that this analysis can help inform that debate.

2.2. Model structure

To address the general question of whether FPAs can benefit indiscriminate fisheries and the specific application to the Tonle Sap, we develop a dynamic spatially-explicit bioeconomic model. The theoretical principles of the model draw on an existing application to marine protection in California (Costello and Kaffine, 2010) and global fisheries (White and Costello, 2014; Costello et al., 2016). To this generalized dynamic spatial model we incorporate several features that are common to indiscriminate freshwater fisheries, including multiple species guilds, species guild migration, and seasonal floodplain and riverine dynamics. We evaluate fish biomass, harvest, and fishing profits over time across the entire system.

Biomass (B) in a connected floodplain and riverine system is modeled using a Pella-Tomlinson model for each species guild s, patch i, and year t. The floodplain is broken apart into discrete spatial patches while the connected river represents a single patch. Each year is composed of two seasons, a high-water (flood) season (Eq. (1)) and a low-water season (Eq. (2)), during both of which the population disperses, grows, and is harvested. The model allows for three species guilds: distant-migrant, non-migrant, and floodplain-migrant. During low-water season, the size of the flooded area decreases and some fraction of the distant-migrant species guild biomass move from the floodplain to the river. During the high-water season, the size of the floodplain increases, and a fraction of the distant-migrant species guilds' biomass returns to the floodplain. Non-migrant species guilds are sedentary and floodplain-migrant species move but stay within the floodplain during both seasons. Growth in each patch is based on species guild-specific growth parameters, g_s and ϕ_s, biomass and dispersal in each patch, and the ratio of the total biomass across all patches to the total carrying capacity of each species guild K_s. There are no species guild interactions.

$$B_{s,i,t+1,H} = \sigma_{s,i,H} B_{s,i,t,L} + \frac{\phi_s + 1}{\phi_s} g_s \sigma_{s,i,H} B_{s,i,t,L} \left(1 - \left(\frac{\sum_i B_{s,i,t,L}}{K_s}\right)^{\phi_s}\right) - F_{s,i,t} \sigma_{s,i,H} B_{s,i,t,L} \quad (1)$$

$$B_{s,i,t,L} = \sigma_{s,i,L} B_{s,i,t,H} + \frac{\phi_s + 1}{\phi_s} g_s \sigma_{s,i,L} B_{s,i,t,H} \left(1 - \left(\frac{\sum_i B_{s,i,t,H}}{K_s}\right)^{\phi_s}\right) - F_{s,i,t} \sigma_{s,i,L} B_{s,i,t,H} \quad (2)$$

Species guild dispersal, $\sigma_{s,i,H}$ and $\sigma_{s,i,L}$ for the high and low-water seasons, includes both immigration and emigration from patch i and all other patches within the system. It is based on species guild-specific site fidelity parameter δ_s, which can vary between 0 and 1, where 0 means fish move freely throughout the system and 1 means fish never move between patches (i.e., the case for the non-migrant species guild). During each season, the biomass of each cell redistributes to each patch based on current biomass in each patch, site fidelity δ_s, and the distance between the centroids of each pair of patches. Fewer patches are available for dispersal during the low-water season. In the case of floodplain-migrant species guilds, dispersal occurs only within the floodplain and fish do not move to the river. In the case of distant-migrant species guilds, a fraction of the total biomass θ_s moves from the floodplain patches to the river patch during each low-water season. During the high-water season, a fraction of the river biomass Ω_s returns to the lake floodplain patches while 1 - Ω_s remains in the river patch. These parameters therefore linearly modify the dispersal parameters $\sigma_{s,i,H}$ and $\sigma_{s,i,L}$ for the distant-migrant species guilds within the floodplain and river patches.

Fishing mortality (F) in each spatial patch and for each species guild is based on fisher cooperation parameter α, which is a continuous value from 0 to 1. An α of 0 corresponds to perfect cooperation (i.e., the village manages fishing mortality towards Maximum Sustainable Yield or MSY), while a value of 1 corresponds to no cooperation (i.e., the village fishes at an open access fishing mortality). We do not model individual fisher behavior or effort, but rather model fishing mortality in various patches based on the management regime in each patch. We also allow for new management scenarios that further adjust fishing pressure based on a management scalar γ that can be applied in specific managed fishing areas (lower values represent more restrictive management). By running repeated simulations over a range of possible γ values, we can therefore find the γ that maximizes either harvest or profit across the system. FPAs are modeled as patches where $F_{s,i,t} = 0$. We assume fishing mortality stays constant over time for a given scenario.

$$F_{s,i,t} = \gamma(\alpha_{s,i,t} F_{OA,s} + (1 - \alpha_{s,i,t}) F_{MSY,s}) \quad (3)$$

$F_{MSY,s}$ is determined for each scenario and spatial management configuration by simulating a range of fishing mortalities over a 100-year time period and finding the optimal fishing mortality that maximizes long-term harvest in final simulation year. This maximum harvest level also corresponds to MSY_s. We also find $F_{MEY,s}$, the maximum economic yield (MEY), by simulating a range of fishing mortalities over a 100-year time period and finding the optimal fishing mortality that maximizes long-term profit in final simulation year. Open access fishing mortality is assumed to be the fishing mortality that leads to an open access biomass that is 30% of the MSY equilibrium biomass, which is used to calculate the fishing cost parameter (see below).

$$F_{OA,s} = F_{MSY,s} \frac{\phi_s + 1}{\phi_s} \left(1 - \frac{0.3^{\phi_s}}{\phi_s + 1}\right) \quad (4)$$

We realize that in practice, it will be difficult for most freshwater fisheries to perfectly manage towards MSY or MEY. However, in practice it may be possible to combine no-take FPAs with one or several regulations that restrict fishing mortality rates (e.g. through size limits, seasonal closures, effort restrictions, or gear restrictions).

Finally, profit (π) is calculated for each species guild, spatial patch, and time period and is based on the harvest, ex-vessel price, variable fishing cost c_s, and cost shape parameter β_s.

$$\pi_{s,i,t} = p_s F_{s,i} \sigma_{s,i,H} B_{s,i,t,L} - c_s F_{s,i}^{\beta_s} \quad (5)$$

Variable fishing cost (c) is therefore calculated based on the assumption that profits are zero at a biomass that is 30% of the MSY equilibrium biomass.

$$c_s = \frac{p_s \frac{F_{OA,s}}{F_{MSY,s}} 0.3 MSY_s}{\left(g_s \frac{F_{OA,s}}{F_{MSY,s}}\right)^{\beta_s}} \quad (6)$$

2.3. General model scenarios

General model scenarios are performed to comparatively test how well FPAs can benefit an indiscriminate freshwater fishery. These

Table 1
Model parameters for general and TSL model scenarios. For the general model scenarios, species guild site fidelity can also range from 0 to 0.8.

Parameter	Species Guild 1	Species Guild 2	Species Guild 3
Species name	Blackfish	Whitefish	Grayfish
Species guild	Floodplain-migrant	Distant-migrant	Floodplain-migrant
Number of high-water cells	415	415	415
Number of low-water cells	89	1	89
Species guild site fidelity (δ_s)	0.6	0.6	0.6
Fraction of the biomass that moves from the floodplain patches to the river patch during each low-water season (θ_s)	0	0.7	0
Fraction of the biomass that moves from the river patch to the floodplain patches during each high-water season (Ω_s)	N/A	0.2	N/A
Growth parameter ϕ_s	0.188	0.188	0.188
Growth parameter g_s	0.021	0.014	0.032
System-wide carrying capacity K_s	2,070,000	8,460,000	1,320,000
Ex-vessel price p_s	3000	9000	3000
Initial biomass relative to virgin biomass	0.3	0.3	0.3

Table 2
Summary of TSL scenarios describing how the fishing mortality is defined for each patch type.

Scenario	F in current FPA patches	F in current CFi patches	F in currently unmanaged patches
No CFis, no current CZs	F_{OA}	F_{OA}	F_{OA}
No CFis, current CZs	0	F_{OA}	F_{OA}
Current F in CFis, current CZs	0	$F_{current}$	F_{OA}
F reduced by 50% in CFis, current CZs	0	0.5 $F_{current}$	F_{OA}
Optimal F for Profit in CFis, current CZs	0	F_{MEY}	F_{OA}
Optimal F for Harvest in CFis, current CZs	0	F_{MSY}	F_{OA}

scenarios therefore vary across three dimensions: FPA size, whether or not high- and low-water seasons are included, and species guilds' site fidelity. We test FPA sizes from 0% to 100% system coverage, with FPAs placed randomly for any given scenario. We test site fidelity parameters ranging from 0 to 0.8, which affects all species guilds equally. We also test the effect of seasonality by either including both seasons, or just the high-water season. For each scenario, we forecast over a 20-year time horizon and look at system-wide harvest and profits in year 20. We parameterize the general model scenarios using the TSL system (see Table 1). The general model scenarios therefore allow us to look at both general trends, and also act as a sensitivity analysis for the TSL-specific scenarios.

2.4. Tonle sap model scenarios

In the TSL model scenarios, we parameterize the model according to specific conditions of the TSL floodplain. To create the spatial structure of the system, Tonle Sap Lake and river was divided into 415 patches. Each existing CFi and government-managed FPA area (known as 'sanctuaries') are their own patch, the river is a patch, and rest of the lake was divided into evenly spaced 5 km by 5 km patches (Fig. 1).

There are many species that live in the Tonle Sap, but they can be broadly categorized into three general species guilds: blackfish, whitefish, and grayfish. The categories are based on the migration patterns of the species. Blackfish and grayfish are floodplain-migrant species and remain in the lake year-round. Whitefish migrate into the rivers during the low-water season, and some move back to the floodplain during the high-water season. Parameters for these species guilds are found in Table 1. Growth parameters and ex-vessel price parameters come from the Inland Fisheries Research and Development Institute of Cambodia (IFReDI), and the movement parameters δ_s, θ_s, and Ω_s are from IFReDI guild descriptions (IFReDI/SciCap, 2018). The total carrying capacity of each species guild is set by assuming current biomass is 30% of virgin biomass, and determining the carrying capacity that would produce a harvest in year 1 roughly equal to the average estimated total current harvest of each species (from IFReDI). Total current harvest of each species is calculated by multiplying the number of fishers in each province by the average annual harvest per fisher in each province and the proportion of each species caught (IFReDI/SciCap, 2018). Total initial biomass of each species is distributed heterogeneously across patches based on the proportional area of each patch.

To model current conditions, we assume patches that are currently FPAs have a fishing mortality of 0 (meaning there is no illegal fishing in the FPAs), patches that are not CZ or CFi have an open access fishing mortality, and the fishing mortality in CFi patches is based on the score they received from a Household Reform Survey that evaluated the level of management cooperation and enforcement effectiveness in each village. The score was used as a proxy for effectiveness of fisheries management, with each CFi receiving a score between 1 and 6 (1 = good management, 6 = bad management), which was then used in Eq. (3) to determine the modeled fishing mortality. A survey score of 1 translates to a fishing mortality of F_{MSY}, while a score of 6 translates to F_{OA}. The single river patch is assumed to be fished at F_{OA}.

We also explore new management scenarios intended to represent current and hypothetical future configurations (Table 2). For each scenario, we model a range of FPA network expansion options up to 100% system coverage. In scenarios where new FPAs are put in place, they are placed randomly in areas that are not currently FPAs or CFis. We run 5 iterations of these random placements for each new FPA scenario.

3. Results

3.1. Generalized model

For the generalized freshwater system, significant gains can be made for both harvest and profit when FPAs up to a certain size are implemented, even without any additional efforts to reduce fishing mortality (Fig. 2). This is true even when FPAs are placed randomly throughout the system; FPA placement optimized for important habitats could lead to even larger gains.

Protection increases both long-term harvest and profit relative to the case with no FPA (see Fig. 2), an effect that truncates and then declines at high levels of protection. Harvest increases by a large increment as protection is initially expanded, then by smaller amounts as maximum harvest is approached. Under the baseline parameterization, harvest is maximized when about 50% of the area is protected. Protection of an area greater than 50% results in declines in both harvest

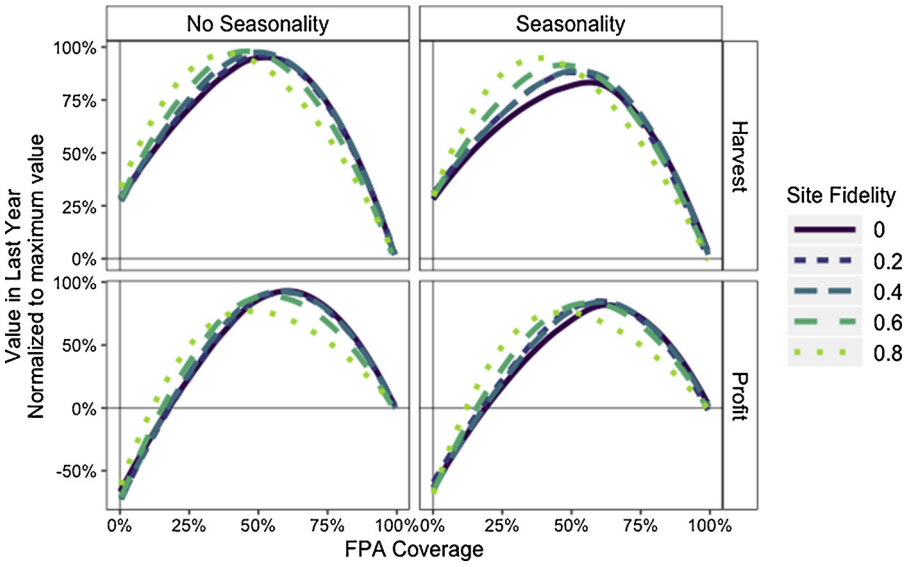

Fig. 2. Generalized model results for a multi-species indiscriminate lake fishery system. Harvest and profit in year 20 are shown under different FPA coverage sizes. Results are shown both with seasonality, which includes high- and low-water periods, and without seasonality. Lines are color coded based on the species guilds' site fidelity. This number represents the fraction of fish that stay in their cell instead of moving to adjacent cells.

and yield, since such a large area is excluded from fishing that no amount of stock increase can make up for the loss in fishing grounds. This is true for harvest and profit (upper and lower panels Fig. 2) and with and without seasonality (left and right panels Fig. 2).

If maximizing profit is the primary goal for fisheries management, we find that FPAs should be slightly larger than if maximizing harvest is the primary goal (top versus bottom panels of Fig. 2). Species guild movement also has an impact on FPA design: species guilds with lower site fidelity (higher movement) need larger FPAs when trying to maximize either harvest or profit. However, optimizing placement to account for the transient nature of mobile species guilds could reduce the need for larger FPAs.

The inclusion of high- and low-water seasonality leads to only minor reductions of the expected harvest or profit for a given FPA size (left versus right panels of Fig. 2). However, because results are aggregate over 20 years, there may be increased seasonal differences in profits with increasing seasonality. High seasonality would be typical of water bodies such as the Tonle Sap, Okavango Delta or rivers with pronounced high and low water stages. Low seasonality would be typical of many lacustrine systems that do not exhibit large intra-annual level variation.

3.2. Tonle sap model results

Consistent with the general results, the specific Tonle Sap results show that increasing protected area from current levels would generally result in large gains in fisheries harvest and profit (Fig. 3), but that this story is more nuanced due to the more detailed structure of the specific model. When we parameterize to the existing conditions in the Tonle Sap, we find that harvest and profit could be maximized when 38% and 56% of the lake are dedicated to FPAs, respectively. Current FPAs cover roughly 5.5% of the lake and our results suggest that this level of protection is too small to generate any substantial benefits to conservation or fishery outcomes. The general model results and the specific Tonle Sap results are described in detail below.

The interplay between FPAs and fishing effort in achieving maximum fishery harvest or profit reveals that 1) optimized fishing mortality for maximum *harvest* for a given protected area coverage is consistently higher than mortality optimized for profit; and 2) at current mortality in the community fishing areas, protection of 40% of the lake or more is required to optimize both harvest and profit (see Fig. 3).

There is a kind of substitution effect between degree of FPA coverage and the level of fishing mortality (i.e. capture) associated with optimal harvest or profit within the CFis: lower FPA coverage requires a

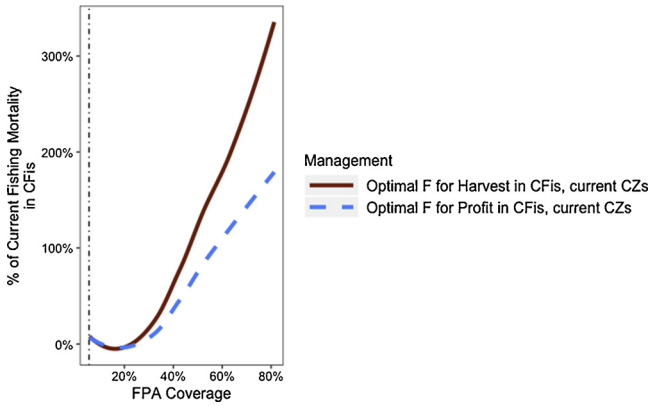

Fig. 3. Harvest and profit at varying combinations of FPA coverage and fishing for the Tonle Sap. FPA coverage and fishing mortality combinations are plotted that achieve either maximum profit or maximum harvest for Tonle Sap in year 20. FPA coverage on horizontal axis, Fishing mortality on vertical axis. Harvest maxima are shown in dark red and profit maxima in broken blue for varying combinations of FPA and management (mortality). Vertical dashed line indicates current FPA coverage. The FPA coverage sizes include the current Conservation Zones as well as additional randomly placed FPAs to achieve a certain coverage percentage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

greater reduction of fishing mortality to maximize either profit or harvest (see Fig. 3). With current FPA coverage of about 5.5% of lake area (vertical dashed line in Fig. 3), fishing effort would have to be greatly reduced, to less than 10% of current fishing mortality, to maximize either harvest or profit, which is likely infeasible.

Conversely, larger FPA coverage would allow for less reduction in fishing mortality, and in fact FPA coverage above a certain point would actually allow for an increase in fishing mortality within the CFis. With the current level of fishery management within the CFis, FPA coverage of roughly 40–60% would be necessary to maximize either harvest or profit. Because a drastic (> 90%) reduction in fishing effort is unlikely on the Tonle Sap, increasing FPA coverage may be a more feasible option for improving fisheries outcomes.

Similar to the generalized results, in the Tonle Sap specific model larger FPAs are necessary if trying to maximize profit rather than harvest for any given level of fishing mortality (compare maximum harvest and profit lines in Fig. 3). This is an important consideration in the Tonle Sap, where subsistence fishers living in poverty may prefer to

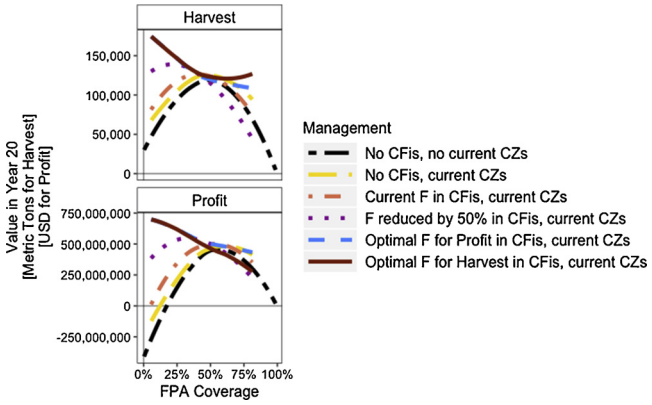

Fig. 4. Harvest and Profit in Tonle Sap in year 20 under different management scenarios and FPA coverage sizes. The FPA coverages include the current conservation zones (CZ) as well as additional randomly placed FPAs to achieve a certain coverage percentage. Line colors correspond to different management scenarios. (For interpretation of the references to colour in the text, the reader is referred to the web version of this article.)

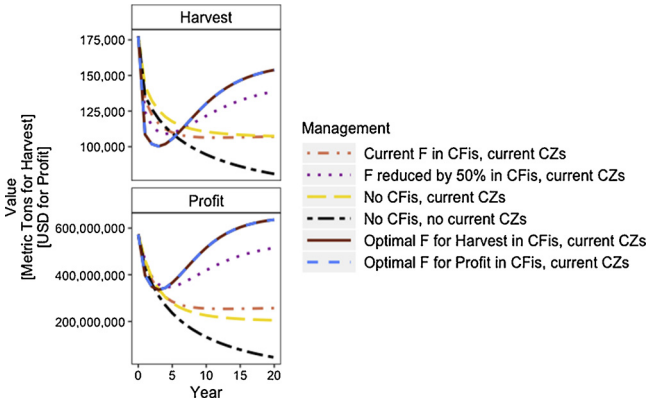

Fig. 5. 20-year harvest and profit trajectories in Tonle Sap in year 20 under with an FPA coverage of 20%. For an FPA size of 20%, the scenarios for optimizing harvest and profit are the same and thus show overlapping trends.

maximize harvest for food and protein, rather than maximizing profit.

We then compared these harvest and profit maximizing management scenarios with the four additional scenarios (see above) approximating incremental progress towards optimal management: 1) open access everywhere (no CFis or CZ); 2) current conservation sanctuaries but open access everywhere else (no CFis), 3) current CFis and conservation sanctuaries, 4) 50% reduction in fishing mortality within CFIs and in the open-access areas, and 5) profit maximizing and 6) harvest maximizing scenarios. For each scenario, we look at fishery harvest and profit across a range of FPA coverages (Fig. 4). This comparison demonstrates the incremental benefits of each layer of management when combined with increasing protected area coverage.

Implementing FPAs alone (yellow line) would increase both harvest and profit relative to a fully open access scenario (black curve). The Tonle Sap currently has small FPAs and CFis that somewhat control fishing mortality (orange curve), which improves the outcome relative to the pure open access outcome (black curve), or just FPAs (yellow curve). Reducing fishing mortality by 50% of current estimated levels (purple curve) would further improve outcomes beyond current conditions (orange curve). Finally, there would be even larger gains to be made if optimal control of fishing mortality is possible (blue and dark red curves).

Even with no additional FPAs, controlling fishing mortality would be most effective at maximizing both harvest and profit (blue and dark red curves). However, if little can be done to control fishing mortality, there are large gains to be made in terms of both harvest and profit by implementing FPAs up to a certain size (black, yellow, and orange curves). With the current level of fishery management within the CFis, protection of a total FPA coverage of 38% would be necessary to maximize harvest, while a total FPA coverage of 54% would be necessary to maximize profit (orange curves). Meanwhile, if the fishing mortality within the CFis could be reduced by 50%, FPA coverage of 28% would be necessary to maximize harvest, while FPA coverage of 31% would be necessary to maximize profit (purple curves). Reduction in fishing mortality therefore also reduces the required FPA size. This holds true even when placing the FPAs randomly or aggregating the area at a single location. Additionally, if current fishing pressure is maintained at its current level, profit will eventually go negative. This could be overcome by implementing FPAs of a certain size.

Finally, we present an example of how harvest and profit evolve over the 20-year time horizon under various management scenarios and an FPA size of 20% (Fig. 5). 20% is a common MPA size recommendation for achieving multiple benefits (e.g., Halpern and Warner, 2003; Green et al., 2014). Fixing FPA coverage at 20% allows us to examine the evolution of benefits over time. Regardless of the management scenario, there is an initial decrease in harvest from current conditions as fishing pressure is necessarily reduced, and given the initial conditions in this model, harvest over time will always be less than what it is currently. However, after 8 years, all improved management scenarios will outperform the forecasted current management scenario. For profit, there will be an initial decrease in profit regardless of management scenario, but the optimal management scenarios for maximizing either harvest or profit will be higher than current conditions after 12 years. Under all improved management scenarios, profit will outperform the forecasted current management scenario by year 5. These results indicate that while harvest and profit will likely continue to decline in the near-term regardless of management scenario, improved management scenarios have the potential to reverse these declines and eventually outperform the current business-as-usual scenario.

4. Discussion

Our results indicate that freshwater protected areas (FPAs) can play an important role in improving or maintaining fisheries output in indiscriminate freshwater fisheries. Because fishing effort in these systems tends to be excessive, we find that profits and protein output of the fishery are maximized when the area of no-take zones in the modeled freshwater system approaches 50% of the total surface area in a stylized FPA model; this result is similar in our much more specific model of the Tonle Sap in Cambodia.

The Tonle Sap is currently very heavily fished, reducing harvest well below what could be achieved with strong management of the fishery. As a result, increasing fish harvest or economic returns requires reducing fishing effort or the area fished, or both. The model results demonstrate that fishing less area can actually increase the amount of fish produced. Increasing area in FPAs or decreasing fishing intensity is a pathway to achieve these benefits.

While it may seem counterintuitive to local communities in Cambodia, they can actually harvest more fish out of the Tonle Sap by fishing less. Whether the reduction in fishing comes through fisheries management such as gear/size restrictions, or through FPAs, reducing fishing will result in increased harvest and greater economic returns. This finding echoes well-established principles in overfished marine systems.

An increase in FPAs could be achieved under existing law in Cambodia. Community fishing areas are required to set aside conservation areas within their boundaries. If these conservation areas within the community fishing areas were established and effectively enforced, our model shows that fisheries production and economic returns would increase. In short, communities need to fish less to feed

more people in the long run.

The fisheries benefits of FPAs demonstrated here may increase social acceptance and support for FPA establishment, as increasing the size of FPAs increases harvest at current levels of fishing, though these benefits will take time to materialize. The FPA literature has focused on the biodiversity benefits of FPAs (Saunders et al., 2002; Suski and Cooke, 2007) due to alarming declines in freshwater biodiversity worldwide (Vörösmarty et al., 2010).

However, real-world uptake of the FPA concept will depend strongly on human benefits associated with implementation of FPAs, and the timing of those benefits (Dehens and Fanning 2018). Communities may not be able to tolerate the short-term loss in production necessary to realize the long-term gains of FPAs. An appropriate role of government, perhaps in cooperation with the international community, would be to provide a fund or other means of sustaining fishing families through the short-term reduction in catch needed to realize the long-term gain. The potential for substantial fisheries benefits demonstrated here provide strong motivation to increase use of FPAs, to the benefit of both people and biodiversity. In particular, a strategy that incorporates both FPAs and catch limits, could optimize fisheries harvest and profit. But where communities composed of subsistence fishing families are tasked with management, as in the Tonle Sap, external assistance may be needed to realize the local and national benefits of FPAs.

The Tonle Sap illustrates that where protein production for poor communities is important, harvest maximization may be a rational fishery management goal, even if it sacrifices substantial economic returns (Szuwalski et al., 2017; Costello, 2017). We found that in our model, a harvest-maximizing fishery has less FPA and higher fishing mortality than a profit-maximizing fishery. As countries develop, they may wish to transition to a profit maximizing goal, which will require somewhat different fisheries management and FPA strategies. Combining FPAs with multiple-use zoning and ecosystem-based management of fisheries may be advantageous in this setting. But even when the goal is to maximzie harvest, increasing FPAs in the Tonle Sap is likely to deliver significant benefits.

We did not explicitly model climate change, but potential changes to rainfall are particularly important to riverine floodplain and flood-pulse systems (Kundzewicz et al., 2008). Monsoonal changes are critical to the Tonle Sap (KC et al., 2017). Climate change will alter the spatial relationship between lake boundaries and internal conservation zones. In low-flood years, the area of no-take zones will be effectively increased relative to the overall size of the lake. Conversely, in high-flood years the area of no-take zones will be effectively decreased. Thus, maintaining an area of FPAs slightly below the maximal profit or harvest may be advantageous. In low-water years this will increase production, due to a higher effective area of protection. No-take protected areas can thus act as a buffer to both sub-optimal management (e.g., Lester et al., 2017) as well as to shocks and larger disturbances such as climate change (McLeod et al., 2009).

The mandate of community fisheries management for the Tonle Sap requires the designation of no-take zones within each of the CFis. Given the long history of poverty and failure of gear restrictions on the Tonle Sap, reducing fishing pressure through gear or size restrictions seems difficult to achieve in practice. On the other hand, implementing the conservation zones of the CFis, which are required under current law but generally unestablished and unenforced, could pay immediate harvest and income benefits. Since current law in Cambodia favors small, decentralized FPAs in community fishing areas (CFi), building the capacity to implement this requirement may be the best option for increasing fishery harvest and incomes of the Tonle Sap.

Here we have presented a relatively simple computational model of fishery-management interactions and show that simple management actions can help to optimize fishery harvest and profit. The complexity of real-world circumstances will undoubtedly limit the feasibility of translating from model to implementation, but the results of our model customized to the Tonle Sap suggest that benefits from FPAs may still materialize in this more complex setting. Further investigations would benefit from evaluating the relative potential of protection of important ecological zones, incorporation of spatial aggregation versus disaggregation and feasibility of protection, as well as evaluating some of the multi-use zoning approaches and levels of restriction that have been extensively explored in the marine realm of protected area design and management.

Management of CFis is still evolving in Cambodia, and the Cambodian government is committed to identifying an equitable solution for effective management planning. There is clear scope for further improvement, and great opportunity to move towards the targets identified here as part of the implementation of community fisheries management that is on-going in Cambodia. Despite the challenges that need to be overcome in real world fisheries management settings, our model demonstrates that combining improved management with FPAs could eventually pay large fisheries dividends for fishing families of the Tonle Sap.

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